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ling or lacerated into many short erect or slightly reflexed segments. Peridial cells, below small and polygonal, above very large and having a flattened conical portion projecting outward and upward from the inner side, sometimes containing a few yellow granules, 18–42 by 15–36μ, wall 2–5μ thick, conspicuously tuberculate, the warts forming short lines or clusters on the surface. Spores yellow or at length pallid, subglobose or oval, regular or slightly angular, 23–32 by 18–25μ, mostly 24–28 by 21–24μ, wall 2–4μ thick, marked with both very fine warts and short, very blunt, round tubercules 1–2μ in diameter, which are wanting on the two attached surfaces but extend around the spore in a band, becoming closely crowded midway between the attached surfaces. Spermogonia amphigenous, scattered, immersed, globose or flask shaped, about 100μ in diameter, scarcely visible except in section.

On *Dalea laxiflora.* Rockport, Rooks County, Kans., June 12, 1888, E. Bartholomew, No. 228.

This is a peculiar and well-marked species. The upper peridial cells on the inner surface overlap somewhat like the scales of a fish, but also project outward. They are also remarkable for their great size. When the æcidia occur on the petioles they cause an enlargement, but on the leaflets scarcely any thickening can be observed. Mr. Bartholomew remarks that the species is "very abundant, making many of the host plants entirely abortive."

A STUDY OF THE ABNORMAL STRUCTURES INDUCED BY USTILAGO ZEÆ MAYS.[1]

(Plates II, III, IV, V, VI, VII.)

By Etta L. Knowles.

The fungus known as *Ustilago Zeœ Mays* is found on Indian corn everywhere. It appears in stem, leaf, grain, and in both staminate and pistilate flowers, producing an abnormal growth of tissue sometimes as large as a man's fist, whitish at first but black when the spores ripen, which is about the time of the ripening of the corn.

In order to understand the changes which are produced by the fungus, a careful study was at first made of the normal structures. Alcoholic material gathered July 19, 1887, was used for this purpose and also for the study of the abnormal structures. Schulze's solution was used for staining the sections and glycerine for mounting them. The drawings were all made with a camera and are on the same scale.

Upon examining the stem it was found to consist of an epidermal system and scattered fibro-vascular bundles, of a somewhat oval form in cross section, between which were the rather large cells of the ground tissue. The latter were hexagonal in cross, and rectangular in longitudinal section, Figs. 1 and 2. Their walls are rather thick and contain numerous thin places which are elliptical in form and lie with their long axes perpendicular to the axis of the stem. Many of these seem to have broken through and formed openings from one cell to the next. The intercellular spaces are small. The size of these cells varies with their position, those midway between two bundles being larger than those immediately adjacent to them.

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[1] This work was carried on under the direction of Prof. V. M. Spalding, in the botanical laboratory of the University of Michigan, 1888.

The bundles are scattered through the ground tissues at somewhat regular intervals, always with the phloëm turned toward the epidermis. Near the periphery of the stem they are packed more closely together, with very little of the ground tissue between, Fig. 3. They are of the form known as the closed collateral bundle. Within the xylem and toward the inner side of the bundle is a space, Fig. 4, *a*. Partially surrounding it is the xylem parenchyma, which is composed of small elements with thinner walls than are found in the adjacent tissue. Back of this canal and partially projecting into it is an annular vessel, *b*. At each side of the bundle is a large duct, *c*, with thick reticulated walls. Between the ducts and back of the annular vessel are thick-walled elements, the tracheides. Between the tracheides and ducts and the external part of the bundle is the phloëm *d*, consisting chiefly of sieve tubes and cambiform cells. The latter, small, thin-walled, square, or rectangular, sometimes narrow or obliquely four sided elements, are distributed among the sieve tubes, which are rather large, thin-walled, polygonal elements. Both sieve tubes and cambiform cells are filled with a granular protoplasm. The elements of the bundle sheath *e* have thick pitted walls. It is developed best at the ends, particularly at the outer end, where it may consist of several layers. At the sides it often borders directly on the ducts. In longitudinal sections, Fig. 5, all of the elements are found to have transverse septa, except those of the bundle sheath, in which they are oblique. The sieve tubes are longer than the cambiform cells, and have the characteristic callous plates. The annular vessels are seen to consist of a very thin-walled portion, which is held open by thick rings placed at nearly regular intervals, *g*. The bundles just under the epidermis are usually somewhat different from those just described in that the larger intercellular space is partially or wholly absent.

The epidermis is made up of cells, which are represented in cross section in Fig. 3, *a*, in longitudinal section in Fig. 6, *a*, and in surface view in Fig. 7, *a*. As seen in the two latter they are elongated cells with slightly sinuous outline and thick pitted walls, the outer of which is somewhat the thicker and covered with a thin cuticle. In longitudinal sections and in those which show surface views there are seen to be two kinds of cells, those already described and short cubical cells. The latter are found usually one at each end of a long cell, but sometimes there are several of them together. The sub-epidermal tissue consists of several layers of sclerenchymatous elements, Fig. 3, *b*, which are similar in appearance to those of the bundle sheath. Numerous stomata were found, each consisting of two guard cells, Fig. 7, *b*, and a pair of accessory cells, *c*. In surface view the former are dumb-bell shaped, fitting closely together at their ends, while the latter are nearly semicircular in outline.

Sections were then taken of a diseased portion of the same stem, of which the normal structure had been studied. The abnormal growth forms a more or less elongated mass at the side of the stem. Fig. 8 is a digrammatic representation of a cross section through a diseased portion, *b*; *a* represents the stem and *c* the outgrowth from it. The part of the stem at *b* seems to be little changed in structure, but at *a* quite the reverse is seen. At the latter point the bundles especially were very much distorted, being swollen to several times their normal size through cell multiplication, and in longitudinal section those lying adjacent to *c* were seen to be sending numerous small branches into it. Getting a very early stage, Fig. 9, the first change noticed was a separation of the epidermis, together with its two or three layers of sub-epidermal tissue, *a*, from the parts lying directly underneath, by one or two layers of cells, *b*, similar to those of the ground tissue and containing starch grains. In the normal stem examined the sub-epidermal layers were so closely connected with the bundle sheath of the peripheral row of fibro-vascular bundles that no line of division could be traced separating the two. Taking sections where the distortion was in all grades of development, it was found that as the abnormal tissue developed this space increased, until, instead of one or two layers of cells, as at first, there was a mass of cells separating them, thick walled in early and thin walled in later stages. The walls of the epidermal cells also became thin. For the most part, then, the abnormal tissue appears to grow in between the epidermal system and the outer row of fibro-vascular bundles, the latter taking part to the extent of sending into it numerous branches. In order to accommodate this great increase of tissue, the epidermal cells stretch and divide and change their form from that seen in Fig. 7 to that seen in Figs. 10 to 14.

The stomata are distorted in the manner shown in Figs. 11, 12, 13, and 14. An attempt was made to trace the changes which take place in the accessory cells from the normal form seen in Fig. 7 *c*, to the distorted form represented in Fig. 14 *b*. Fig. 14 was from a section cut from a place where the spores were nearly ripe, while Figs. 11, 12, and 13 were taken from the surface of tissue which was not so well developed, and represent three forms intermediate between the normal form Fig. 7 and the distorted form Fig. 14.

The cells of the ground tissue were found to be different in form according to their position. Those in the region of active growth, that is, in the region adjacent to the normal part of the stem, Fig. 8 *d*, were seen to be of the form of those represented in Fig. 15, very thin-walled, the long axes of the cells lying parallel to a tangent drawn to the nearest point of the original stem. Each was completely filled with material for growth. Passing farther out this form gradually changes first to that represented in Fig. 16, then to a form like those in Fig. 17, then to smaller cells again, and covering all the epidermal cells, as shown in Fig. 18. The cells described above all had thin walls, without pits or openings. In most of them the nucleii were very large and conspicuous, especially in those represented in Fig. 18. Abnormal fibro-vascular bundles ran through the tissue, and adjacent to them the cells of the ground tissue were elongated in the direction of the length of the bundle.

In Fig. 19 a bundle is represented in which the distortion has not been carried very far. It has become a little broader by cell-multiplication, and the xylem parenchyma and tracheides as well as all of the phloëm have become very thin-walled, and give the reaction for cellulose with Schultze's Solution. In the normal structure the two former were composed of liquefied elements. Large nucleii were observed in a great many of the cells of the xylem parenchyma and in one or two cases in the sieve tubes. The cells of the bundle sheath have multiplied at both ends of the bundle, and in a more distorted bundle than the one represented were seen to also have become thin-walled. In stages a little farther on, cells which looked like those of the ground tissue, and which were filled or partially so with starch, had grown in and separated the bundle into little groups or bundles of thin-walled cells. These branches passed out into the abnormal growth, and these branched again, forming altogether a sort of tree-like organ for the support and nourishment of the delicate tissue through which it runs. Figs. 20 *a* and 21 show longitudinal sections of the bundles as they appear in this tissue. They are composed of short, narrow, thin-walled cylindrical cells, arranged end to end. Nucleii are conspicuous in most of them, and all are filled with a finely granular substance which colors yellow with Schultze's Solution. In Fig. 21 the bundle has thrown off a slender branch at *a*. The walls of these cells had no markings, and the cells themselves appeared very much like cambiform cells, except that they were shorter, and contained conspicuous nucleii. In the normal tissue nucleii were not observed in either sieve tubes or cambiform cells. In some of the bundles similar to those figured in 20 and 21 there were one or two layers of cells at each edge of the bundle which were small and thin-walled, but showed reticulated and pitted markings. In Fig. 22 a cross section of one of these bundles is represented. In them the elements are so changed that phloëm can not be distinguished from xylem, and there are no large elements. Where the large pitted ducts run into the abnormal tissue, which usually they do not, they take a course separate from the bundles and have very grotesques forms, changing direction constantly.

The observations made upon the fungus which causes these changes agree with the descriptions which have been repeatedly given of it. It consists of a thick-walled mycelium tube, the lumen of which is not constant in diameter, but in some places widens out and in other places is almost or apparently quite closed. The thickness of the mycelium filament also varies constantly. These coarse, tough threads are found in different parts of the stem, some at the center, others nearer to the periphery, running between the cells or into them, and with their sharp end pushing directly through the thickest walls, Fig. 24.

In fruiting, the mycelium forms a great number of short slender branches. Great masses of these are found in little nests in the abnormal tissue, Fig. 20, also Fig. 8. They are more slender and delicate than the mycelium already described and are generally of quite irregular form. Fig. 23 represents a much branched mycelium filament, which appeared in a break in a section. It appeared to have pushed its way in between the cells and not to have penetrated them. The slender filaments of these masses swell up into a form like that represented in Fig. 25, except that in many cases—indeed in most cases—the filaments lose their individual form and are more or less blended in a gelatinous, shapeless mass. Rounded places with little masses of rich protoplasm, Fig. 25 *a*, indicate spores in an early stage of formation. All stages may be found in the same mass. Fig. 26 shows later stages, where the ends of the filaments appear club-shaped and within are seen the almost ripe spores. The mature spore, Fig. 27, is one celled with two walls; the outer thick, brown, and covered with spines. The inner delicate and transparent.

From the comparatively small number of species in which abnormal changes under the influence of parasitic fungi have been carefully studied, it is hardly possible as yet to venture on any general or theoretical statements concerning the pathological changes induced by such parasites. It seems best therefore, in the present instance, to simply recapitulate the injuries occasioned to the host by the fungus in question, since it is only by multiplied observations of the same kind that sufficient data can be gathered for a more general conception of the relations of parasite and host.

The changes observed in the stem of *Zeæ Mays* are briefly as follows:

An extraordinary hypertrophy of the parts of the host where spore formation takes place, the irregularity of which gives rise to peculiar and conspicuous distortion.

Microscopic examination shows: (1) Great multiplication of cells near the periphery; (2) decrease in thickness of cell walls and, in case of the bundles, of the size of the elements; in many cases a decrease in the size of the cells of the ground tissue also; (3) distortion of the stomata, particularly of the accessory cells, (4) a breaking up of the bundles and a changing of their elements, so that in many cases phloëm can not be distinguished from xylem; (5) a marked increase of cell contents.

31. Three spores seen in optical section showing spines, thickness of wall and slightly granular and guttate ? contents, x 500.

(Figs. 32–40 showing germination of spores of *Ustilago boutelouæ* in distilled water on slide in damp chamber 24 hours at 37° C.; collected December 20, 1888, germinated February 20, 1889.)

32. Spore showing cleft in the wall and young promycelium, x 500.
33. Spore bearing a branched promycelium which has split the cell-wall and about to produce a sporidium on the side (?), x 500.
34. Spore showing two promycelia, the one scarcely developed, x 500.
35. Spore seen in optical section showing a slender promycelium apparently connected with the contained gutta, x 500.
36. A spore with a more mature promycelium which is either branched and bearing a sporidium at the end of the branch, or a primary sporidium is producing a secondary one, x 500.
37. A free sporidium budding, x 500.
38. A promycelium broken off from the spore, bearing two sporidia from below the septa, x 500.
39. A free promycelium bearing a single sporidium, x 500.
40. A slender free promycelium producing a single sporidium, x 500.

PLATE II.

Fig.

1. Cross-section of cells of normal ground tissue; *a*, intercellular spaces.
2. Longitudinal section of cells of normal ground tissue.
3. A section of a portion of the normal epidermis with the underlying parts; *a*, epidermal cells; *b*, sub-epidermal layers; *c*, cells of the ground tissue.

PLATE III.

4. Cross-section of a normal fibro-vascular bundle; *a*, intercellular canal; *b*, annular vessel; *c*, pitted ducts; *d*, phloëm; *e*, elements of the bundle sheath.
5. Longitudinal section of a normal bundle; *a*, cells of ground tissue; *b*, elements of bundle sheath; *c*, cambiform cells; *d*, sieve tubes; *e*, tracheid; *f*, portions of an annular vessel; *g*, intercellular passage; *h*, wood parenchyma.

PLATE IV.

6. Longitudinal section of normal epidermis; *a*, large; *b*, small cells of epidermis; *c*, sub-epidermal cells.
7. Surface view of normal epidermis; *a*, large; *d*, small cells; *b*, guard cells; and *c*, accessory cells of the stomata.
8. Diagram of a section of a stem with the abnormal growth; *a*, *b*, stem; *c*, abnormal growth; *e*, bundles; *d*, region of active growth. The light shading represents ground tissue cells, the dark shading masses of spores, and the lines in *c* the bundles sent out to the abnormal growth.
9. Section similar to that represented in Fig. 3, except that it is slightly distorted; *a*, epidermal and sub-epidermal layers; *b*, ground tissue cells; *c*, portion of a bundle.
10. Surface view of epidermis of abnormal tissue; *a*, epidermal cell; *b*, nucleus.

11, 12. Surface view of abnormal tissue showing distortion of stomata; *a* guard, cells; *b*, accessory cells; *c*, epidermal cell.

PLATE V.

13, 14. Surface view of abnormal tissue showing distortion of stomata; *a*, guard cells; *b*, accessory cells; *c*, epidermal cell.
15. Cross-section of cells of abnormal ground tissue in region of active growth, showing nucleii.
16. Cross-section of the same a little nearer the periphery nucleii not so conspicuous, and are not represented.
17. Cross-section of the same still nearer the periphery.

PLATE VI.

18. Cross-section of the same near the periphery with *a*, the epidermal cells.
19. Cross-section of a distorted bundle; *a*, intercellular canal; *b*, annular vessel; *c*, pitted duct; *e*, element of bundle sheath; *f*, wood parenchyma.

PLATE VII.

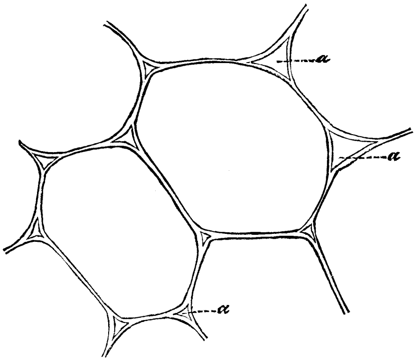
20. A section in abnormal tissue showing *a*, longitudinal section of a bundle, also a mass of mycelium filaments in early fruiting stage.
21. Longitudinal section of a more typical abnormal bundle; *a*, branch of the bundle.
22. Cross-section of the abnormal bundle.
23. Mycelium filament.
24. Mycelium filaments running through cells of the ground tissue.
25. Early stage of spore formation.
26. Later stage of spore formation.
27. Mature spore.

-- = $.01^{mm}$, scale to which the figures are drawn.

PLATE VIII.

Fig. 1. Upper surface of pileus of *Mucronoporus tomentosus*, Fr.
2. Lower surface of same.
3. Section of pores showing the projecting points or spines.
4. One of these spines more highly magnified.
5. Spine with a bifid tip.

Journal of Mycology, U. S. Department of Agriculture, 1889. PLATE II.



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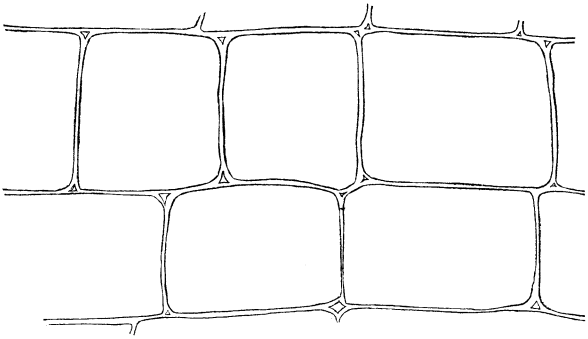

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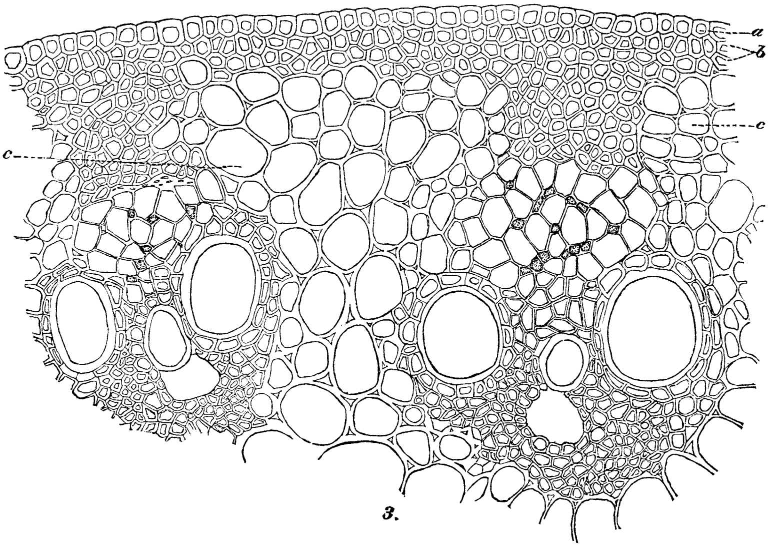

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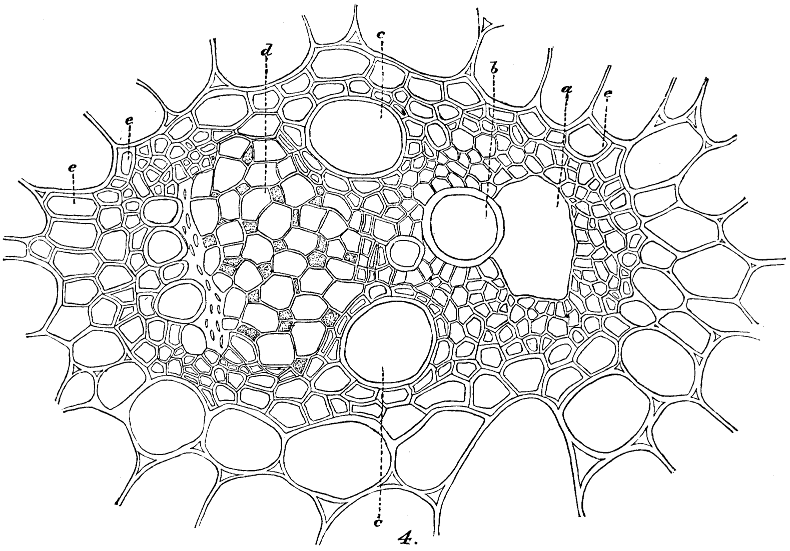
KNOWLES ON USTILAGO ZEÆ-MAYS.



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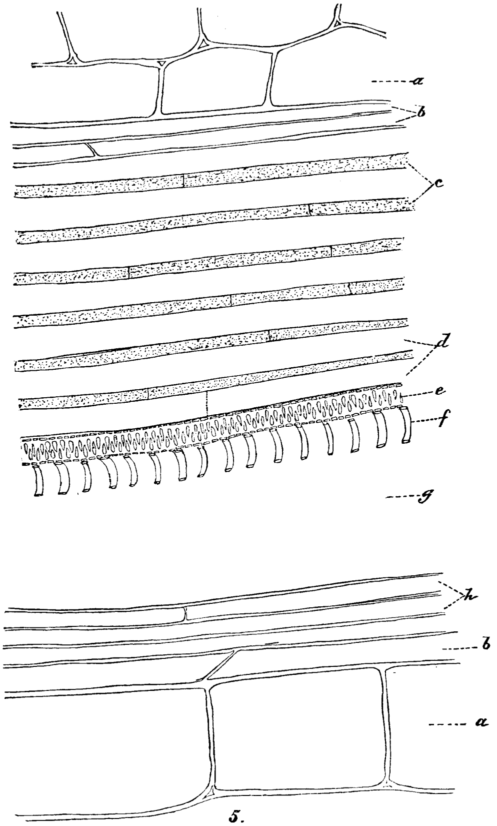

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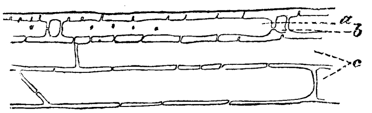

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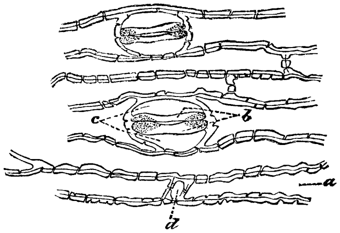

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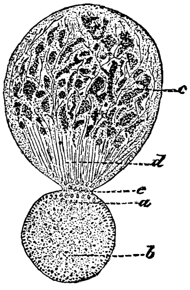

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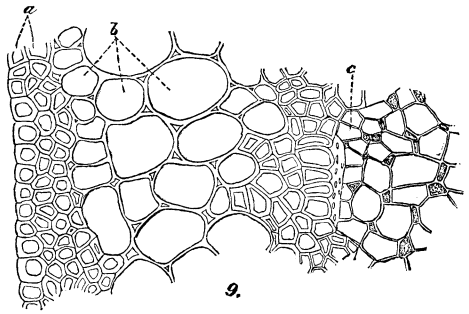

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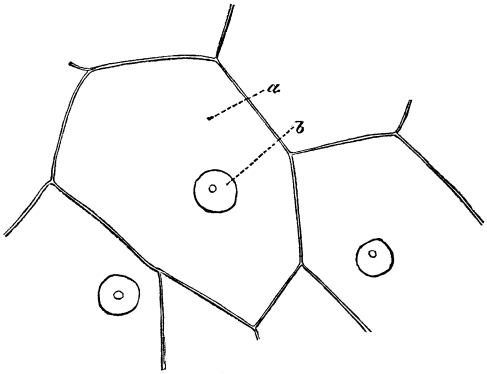

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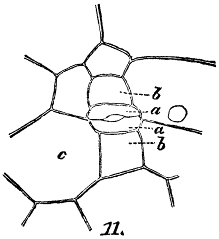

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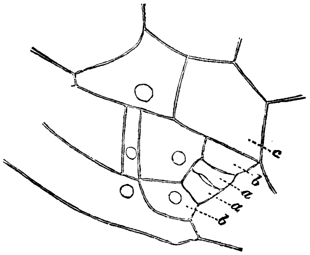

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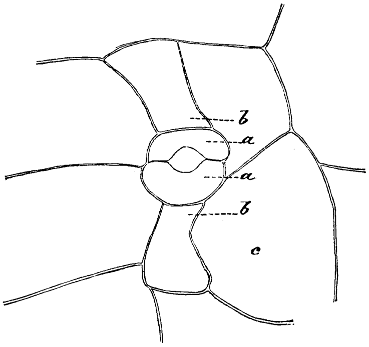

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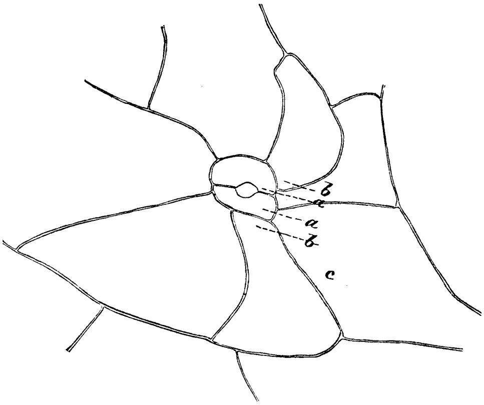

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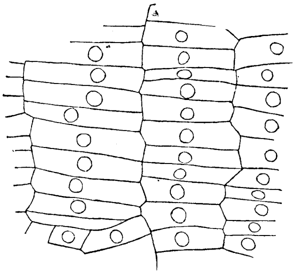

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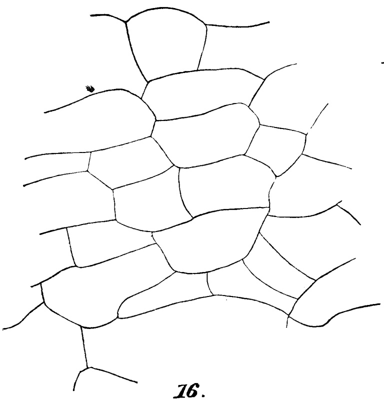

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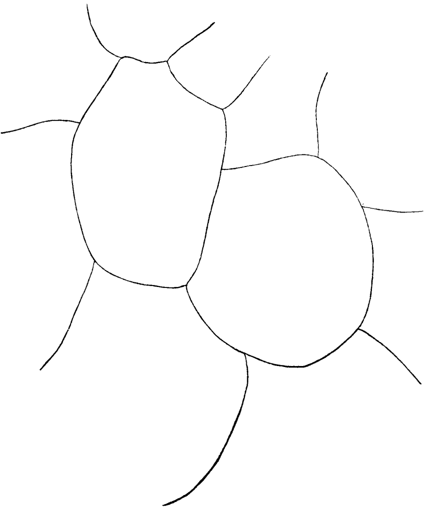

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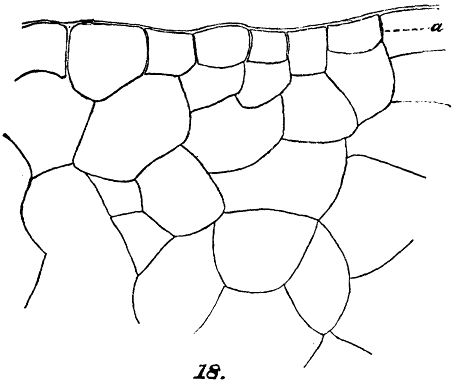

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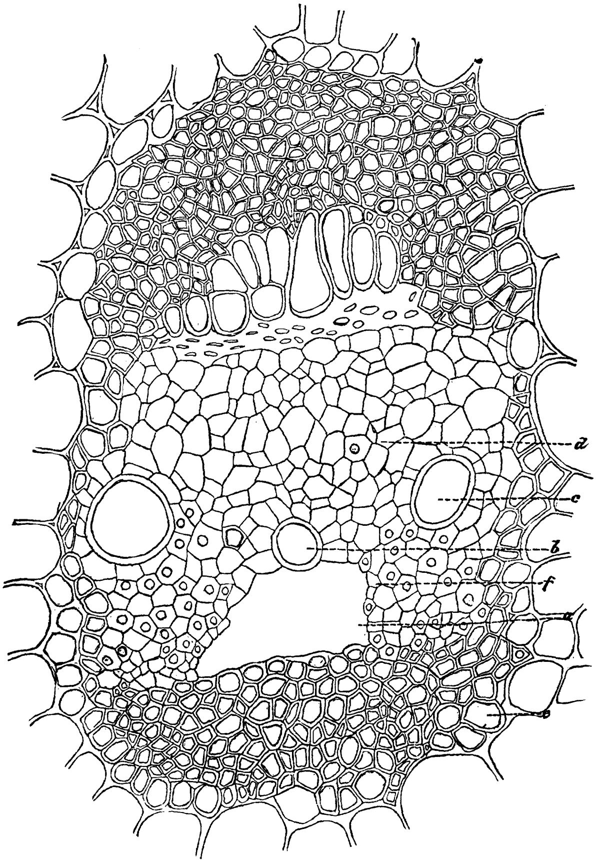

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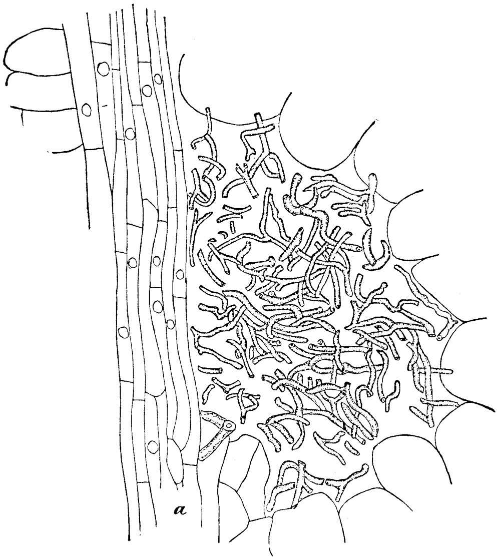
Journal of Mycology, U. S. Department of Agriculture, 1889.

PLATE VII.



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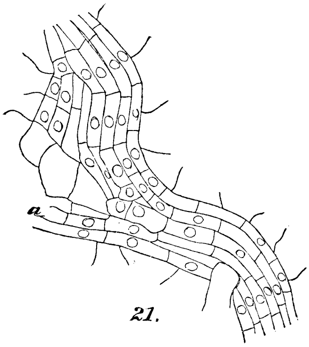

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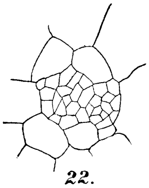

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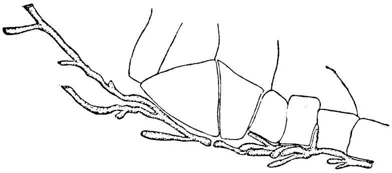

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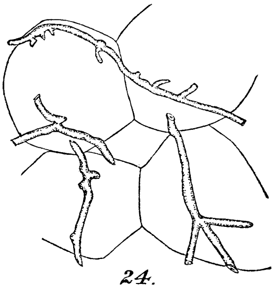

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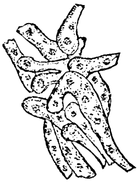

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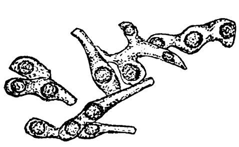

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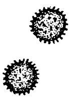

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